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# Counterintuitive density-dependent growth in a long-lived vertebrate after removal of nest predators

## Abstract

Examining the phenotypic and genetic underpinnings of life-history variation in long-lived organisms is central to the study of life-history evolution. Juvenile growth and survival are often density dependent in reptiles, and theory predicts the evolution of slow growth in response to low resources (resource-limiting hypothesis), such as under densely populated conditions. However, rapid growth is predicted when exceeding some critical body size reduces the risk of mortality (mortality hypothesis). Here we present results of paired, large-scale, five-year field experiments to identify causes of variation in individual growth and survival rates of an Australian turtle (*Emydura macquarii*) prior to maturity. To distinguish between these competing hypotheses, we reduced nest predators in two populations and retained a control population to create variation in juvenile density by altering recruitment levels. We also conducted a complementary split-clutch field-transplant experiment to explore the impact of incubation temperature (25° or 30°C), nest predator level (low or high), and clutch size on juvenile growth and survival. Juveniles in high-recruitment (predator removal) populations were not resource limited, growing more rapidly than young turtles in the control populations. Our experiments also revealed a remarkably long-term impact of the thermal conditions experienced during embryonic development on growth of turtles prior to maturity. Moreover, this thermal effect was manifested in turtles approaching maturity, rather than in turtles closer to hatching, and was dependent on population density in the post-hatching rearing environment. This apparent phenotypic plasticity in growth complements our observation of a strong, positive genetic correlation between individual body size in the experimental and control populations over the first five years of life ( $r_G +0.77$ ). Thus, these Australian pleurodiran turtles have the impressive capacity to acclimate plastically to major demographic perturbations and enjoy the longer-term potential to evolve adaptively to maintain viability.

## Keywords

adaptive plasticity, Australia, density dependence, *Emydura macquarii*, freshwater turtle, genetic correlation, growth optimization, juvenile growth, predator removal experiment, reaction norm, survival

## Disciplines

Ecology and Evolutionary Biology | Evolution | Population Biology

## Comments

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## COUNTERINTUITIVE DENSITY-DEPENDENT GROWTH IN A LONG-LIVED VERTEBRATE AFTER REMOVAL OF NEST PREDATORS

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**Abstract.** Examining the phenotypic and genetic underpinnings of life-history variation in long-lived organisms is central to the study of life-history evolution. Juvenile growth and survival are often density dependent in reptiles, and theory predicts the evolution of slow growth in response to low resources (resource-limiting hypothesis), such as under densely populated conditions. However, rapid growth is predicted when exceeding some critical body size reduces the risk of mortality (mortality hypothesis). Here we present results of paired, large-scale, five-year field experiments to identify causes of variation in individual growth and survival rates of an Australian turtle (*Emydura macquarii*) prior to maturity. To distinguish between these competing hypotheses, we reduced nest predators in two populations and retained a control population to create variation in juvenile density by altering recruitment levels. We also conducted a complementary split-clutch field-transplant experiment to explore the impact of incubation temperature (25° or 30°C), nest predator level (low or high), and clutch size on juvenile growth and survival. Juveniles in high-recruitment (predator removal) populations were not resource limited, growing more rapidly than young turtles in the control populations. Our experiments also revealed a remarkably long-term impact of the thermal conditions experienced during embryonic development on growth of turtles prior to maturity. Moreover, this thermal effect was manifested in turtles approaching maturity, rather than in turtles closer to hatching, and was dependent on population density in the post-hatching rearing environment. This apparent phenotypic plasticity in growth complements our observation of a strong, positive genetic correlation between individual body size in the experimental and control populations over the first five years of life ( $r_G \sim +0.77$ ). Thus, these Australian pleurodiran turtles have the impressive capacity to acclimate plastically to major demographic perturbations and enjoy the longer-term potential to evolve adaptively to maintain viability.

**Key words:** adaptive plasticity; Australia; density dependence; *Emydura macquarii*; freshwater turtle; genetic correlation; growth optimization; juvenile growth; predator removal experiment; reaction norm; survival.

### INTRODUCTION

Life-history traits vary with environmental factors such as predation (Tinkle and Ballinger 1972, Reznick et al. 1996, 2001), food (Dunham 1978, Niewiarowski and Roosenburg 1993, Bernardo 1994, Bronikowski and Arnold 1999), temperature (Schultz et al. 1996), and overall climate (Berven and Gill 1983). Such environmentally induced phenotypic variation (phenotypic plasticity) can arise from altered developmental trajectories and embryonic growth rates, particularly in oviparous organisms. Still, the ecological and evolutionary significance of plasticity for most traits remains obscure (Via et al. 1995).

Understanding how phenotypic variability arises in response to the environment could help to ascribe trait variability to adaptation (Lorenzon et al. 2001). Phenotypes can be expressed in two ways in response to the environment. Different environmental conditions may induce phenotypic variation through its influence on gene expression (phenotypic plasticity) or through differential selection on the traits and their associated genotype (genetic polymorphism) (Lorenzon et al. 2001). Transplant experiments provide a robust technique to assess phenotypic variation caused by plasticity: if two genotypes express the same phenotype in the same environment, then phenotypic differences observed under natural conditions result from phenotypic plasticity (Niewiarowski and Roosenburg 1993, Rhen and Lang 1995, Schultz et al. 1996, Sorci et al. 1996). Conversely, if phenotypic differences between genotypes are maintained across different environments, the variability derives from a heritable polymorphism (Lorenzon et al. 2001).

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Whether plasticity is locally adaptive is difficult to demonstrate (Smith-Gill 1983, Gotthard and Nylin 1995) because fitness associated with a trait is challenging to estimate in different environments (Lorenzon et al. 2001). By definition, life-history traits have a large effect on fitness, including juvenile growth and survival rates (Huey and Stevenson 1979, Dunham et al. 1989, Sinervo and Adolph 1994). Variation in juvenile survival can hardly be compensated by variation in other life-history traits, such as fecundity or adult survival, to ensure a similar fitness over the entire life cycle (Sorci et al. 1996, Boudjemadi et al. 1999). Body size and growth rate affect fitness directly, as well as indirectly through age and size at maturity, fecundity, and/or adult survival (Adolph and Porter 1993, Berrigan and Charnov 1994, Sibly and Atkinson 1994). Thus, juvenile growth and juvenile survival are important fitness components, such that low values will reflect low fitness.

Juvenile growth and survival may be density dependent in reptiles (Massot et al. 1992) because of competition for food (Wilbur and Collins 1973). Besides resource availability, social interactions can affect feeding and growth rates of reptiles and amphibians (Andrews 1982). For example, in laboratory-staged dominance interactions, larger neonatal snapping turtles often win contests for food items over smaller ones (Froese and Burghardt 1974).

Theory predicts the evolution of slow growth in response to low resources (resource-limiting hypothesis), such as under densely populated conditions (Arendt and Reznick 2005). However, rapid growth is predicted when exceeding some critical body size reduces the risk of mortality. For example, predation levels are substantial on small hatchling turtles (Janzen et al. 2000) and theories of density-dependent natural selection suggest that intraspecific competition will favor juveniles of high competitive ability (Svensson and Sinervo 2000); hence, rapid juvenile growth would be favored by selection under both conditions (mortality hypothesis). Both of these hypotheses concern different life-history phenotypes with respect to age-specific allocation of energy, but they yield opposing predictions of potential growth rates (Reznick et al. 1996, 2001, Arendt and Reznick 2005). The resource-limiting hypothesis concerns a reduction in energy, whereas implicit in the mortality hypothesis is a reallocation of energy, or change in ecological, behavioral, or physiological traits, which is conducive to selection and possible life-history evolution. To address the ecological and evolutionary significance of a variation in growth rates, it is necessary to distinguish between the two competing hypotheses.

Freshwater turtles provide an excellent system to experimentally test for local adaptation of growth rates to environment. First, turtles are oviparous and eggs can be distributed across a range of incubation conditions to test for the effect of developmental environment on phenotype (Ewert 1985, Packard and Packard 1988). Second, some species inhabit essentially closed popula-

tions and produce relatively large clutches of eggs, which is ideal for split-clutch transplants of hatchlings into different environments. Last, although population densities are often high (Spencer and Thompson 2005), nest predation rates are also generally high (Congdon et al. 1983, but see Bowen and Janzen 2005), meaning that recruitment and juvenile densities are typically low (Spencer 2002a, Spencer and Thompson 2005). Thus any reduction in nest predators could lead to a large increase in recruitment levels, which is conducive for density-dependent processes and interactions.

Here we present results of paired, large-scale, five-year field experiments to identify causes of variation in individual growth rates of a long-lived turtle (*Emydura macquarii*) prior to maturity (see Plate 1). To distinguish between resource-limiting and mortality hypotheses, we greatly reduced nest predators in two populations and did not manipulate a control population to create variation in juvenile density by altering recruitment levels. We also conducted a complementary split-clutch field-transplant experiment to explore the impact of incubation temperature (25° or 30°C), nest predator level (low or high), and clutch size on juvenile growth. We then interpreted results of these two experiments in the context of findings from a long-term demographic study to assess predictions of the competing hypotheses. Specifically, we would expect reduced individual growth rates in high-recruitment (low-predator) populations if resources are limiting. Alternatively, we would expect rapid individual growth in high-recruitment populations if juvenile survival is positively associated with body size.

## METHODS

Study sites were located in the upper Murray River of southeastern Australia (for complete descriptions, see Spencer [2002a, b]). Four populations (Snowdon's, Hawksview, Bankview, and Cook's lagoons) of *Emydura macquarii* on the Murray River in Australia have been studied since 1996. Over 90% of turtle nests are destroyed by introduced foxes (Thompson 1983, Spencer 2002a), and these populations have been part of a large project investigating the full impact of foxes on turtle demography (Spencer and Thompson 2005) and behavior (Spencer 2002a, Spencer and Thompson 2003). *Emydura macquarii* is an omnivorous turtle that is heavily reliant on adult turtles for population stability (Spencer and Thompson 2005). The juvenile population is extremely small, and even minor reductions in nest predation rates can potentially increase recruitment significantly.

We used a BACI-designed (Before-After-Control-Impact; Underwood 1997) fox removal program to determine the impact of foxes on freshwater turtle population dynamics (see Spencer and Thompson 2005). Essentially, fox numbers were monitored in all sites from July 1996 to January 1999, using spotlight counts conducted over 4–7 consecutive nights each month



PLATE 1. Hatchling *Emydura macquarii*. Photo credit: R. Spencer.

between August and November, and every second month between January and May. Foxes were removed, using spotlight shooting and a baiting program, from around two lagoons (fox removal sites: Snowdon's and Hawksview) after the first nesting season, whereas foxes were continually monitored around another lagoon (control site: Bankview). Each site was chosen randomly as a removal or control site. We monitored nest predation rates around each lagoon and conducted a large capture-mark-recapture (CMR) program of each (except Cook's) turtle population to determine stage-specific life-history traits (growth, fecundity, and survival) between September and March of each year from 1996 to 1999 and in February 2001 and 2002 (see Spencer 2002b, Spencer and Thompson 2005).

Turtles were predominantly captured in hoop traps with a trap entrance in an inward rectangular funnel (300 mm wide and 120 mm deep). Traps were baited primarily with ox liver placed into bait cages in the center of the trap. Trapping was carried out for 10–18 days each month within the lagoons between September and March of each year from 1996 to 1999 and in February 2001 and 2002 (Snowdon's lagoon was also trapped in January–March 1995). Each captured turtle was sexed (Cann 1998) and weighed to the nearest 25 g using a 10-kg spring balance. Smaller turtles (<500 g) were weighed to the nearest 10 g using a 1-kg spring balance. Curved and straight carapace (CL) and plastron (PL) lengths were measured to the nearest 1 mm with a tape measure and calipers. Each turtle was

given a unique combination of notches in the marginal scutes and underlying bone (Thompson 1982) with a 10-mm electric grinder (Ryobi, Sydney, NSW, Australia) or bastard file. Marked turtles were released within 12 h at their point of capture.

We developed separate growth curves for each population to determine if juvenile growth varied among populations both before and after fox removal. Changes in juvenile growth have the largest effect on the growth coefficient ( $k$ ), but differences in size between adults may be more related to asymptotic size ( $a$ ) or to indeterminate growth than they are to differences in growth rates (Stamps et al. 1998). Both parameters were derived from von Bertalanffy growth equations (Spencer 2002b). Fabens (1965) derived the growth-interval equation of the von Bertalanffy model:

$$L_2 = a - (a - L_1)e^{-k(dt)}$$

where  $L_1$  is straight plastron length at first capture,  $L_2$  is straight plastron length at recapture, and  $dt$  is time in years between capture dates. Growth occurs during the warmer months of the year (November–May), which corresponds to the trapping season. Growth data of turtles captured one or more trapping seasons apart were included in the model. Growth trajectories were estimated from plastron lengths of recaptures using nonlinear regression of the interval equation to estimate the parameters  $a$  (asymptotic size) and  $k$  (growth coefficient). JMP 5.1 (SAS Institute 2003) was used for nonlinear regression procedures. We compared esti-

mates of  $k$  and  $a$  from each population both before and after fox removal began.

#### Transplant experiment

Gravid female *E. macquarii* were captured in Mulwala lagoon (~100 km downstream of the focal populations) and were induced to lay their eggs by a subcutaneous intramuscular injection of 2 mL of oxytocin (Syntocin, Ilium) in the thigh (Ewert and Legler 1978). Injected turtles were placed in enclosed cardboard containers, where most began to oviposit within 30 min. Eggs were marked using an HB graphite pencil and were placed into a mixture of two parts vermiculite to one part water by mass (approximating  $-370$  kPa) in foam containers ( $1000 \times 400 \times 350$  mm). The female's number and the egg number (in order from oviposition) were marked on each egg. All eggs were transported to the University of Sydney within 24 h of collection. Clutches were randomly incubated at  $25^\circ$  or  $30^\circ\text{C}$ . Because *E. macquarii* does not have temperature-dependent sex determination (Thompson 1988), male and female offspring were produced in both incubation treatments. Distilled water was used to compensate for small water losses from the incubation boxes.

Hatchlings (see Plate 1) were toe-clipped with unique combinations that distinguished between clutch and temperature treatments. Only one toe from each foot was clipped (webbing rarely disrupted) and no more than three feet were clipped on each individual. Hatchlings were weighed and their plastron and carapace lengths and widths were measured before release. In total, 1218 hatchling turtles were marked and released at the beginning of 1997 and 1998 into both Hawksview (fox removal) and Bankview (control) lagoons. We designed the experiment such that hatchlings from each clutch were released into both lagoons. Recaptured hatchlings were identified (from toe clippings) and remarked as part of the general CMR program in both lagoons (see Spencer 2002b, Spencer and Thompson 2005).

The data set comprised CMR history profiles in five trapping periods (years) for each population. We analyzed growth of juvenile turtles by comparing the plastron lengths of released hatchlings over this time using ANCOVA with density, incubation temperature, and age as factors and plastron length at hatching as a covariate. Turtles captured multiple times were only included once (first capture) in the analyses. We used the Holm-Sidak pairwise multiple comparison procedures to compare between treatment groups. Raw data were  $\ln$ -transformed. Finally, we used paired  $t$  tests to compare the size distributions of turtles captured in both Bankview (low-recruitment) and Hawksview (high-recruitment) lagoons before (January 1997) and five years after (January 2002) fox removal. SigmaStat 3.1 (SPSS 2004) and SYSTAT 10.0 (SPSS 2000) were used for these statistical procedures.

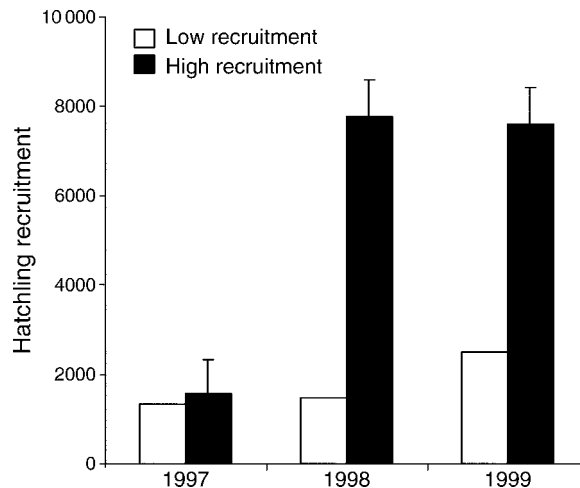


FIG. 1. Annual hatchling recruitment (mean  $\pm$  SE) into low-recruitment and high-recruitment populations of the turtle *Emydura macquarii*, 1997–1999. Removal of foxes (high-recruitment treatment) caused a 400% potential increase in hatchling recruitment.

We also took advantage of the split-clutch experimental design to estimate cross-environment genetic correlations ( $r_G$ ) in body size for each trapping period. Consistently high values (i.e., closer to +1) would imply that body size and growth possess a substantial heritable basis to respond evolutionarily to selection in a similar manner, regardless of rearing environment. We adopted a family mean correlation approach (reviewed in Astles et al. 2006) in which  $r_G$  is approximated by calculating Pearson product-moment correlations between clutch means in both rearing environments (i.e., Hawksview and Bankview). Turtles exhibit extensive multiple paternity, yet we conservatively assumed that clutch mates were full siblings. The presence of half siblings would render the true  $r_G$  values even higher, although non-genetic maternal effects could inflate the estimates. Even so, the empirical literature suggests that employing the family means method is a valid, conservative approach for estimating  $r_G$  values across environments (Astles et al. 2006).

Survival ( $\phi$ ) and capture ( $p$ ) probabilities of turtles in each population were estimated and modeled following CMR methodology (Lebreton et al. 1992) and the method developed by Pradel (1996) using the program MARK (White and Burnham 1999). Plastron length (mm) at hatching was included as an individual covariate in the model. To select the most appropriate model for describing demographic temporal variation, we used a bias-corrected version of Akaike's Information Criterion,  $AIC_c$ . We tested for overdispersion and adjusted the  $AIC_c$  value ( $QAIC_c$ ) using an estimate of the variance inflation factor,  $\hat{c}$  (Anderson et al. 1994). Models were compared by  $QAIC_c$  value, and we retained the most parsimonious one (lowest  $QAIC_c$ ; Anderson et al. 1994).

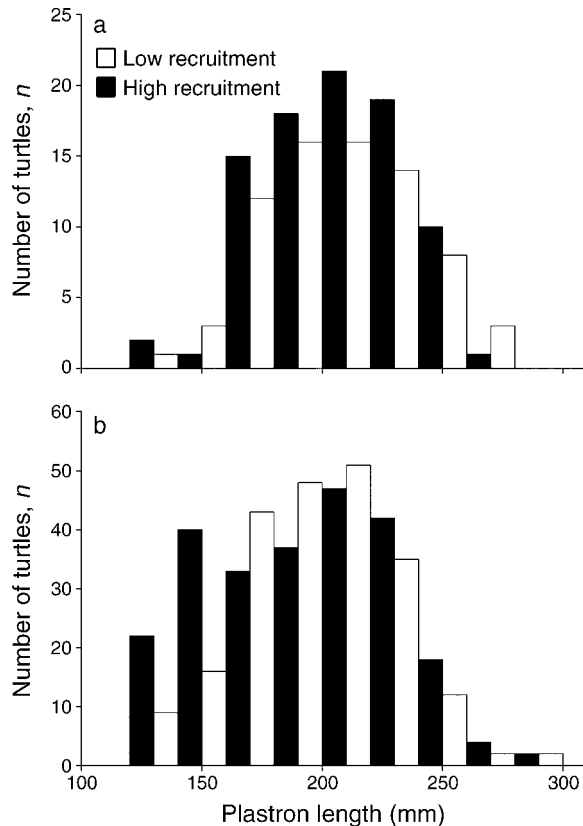


FIG. 2. Size distribution histogram for low-recruitment and high-recruitment sites from a catch (a) in February 1997 and (b) in February 2002. Hatchling turtles were released in February 1997 and 1998.

## RESULTS

### Density

Female population sizes of Bankview, Hawkview, and Snowdon's lagoons were 615, 587, and 632 female turtles, respectively, and average fecundity was calculated at 24 eggs/yr (Spencer 2002b, Spencer and Thompson 2005). Nest predation rates were 85–93% at all sites prior to fox removal. After fox removal, nest predation rates fell below 50% in treatment sites, but remained above 83% in the control site (Spencer 2002a).

Under conditions of high nest predation, potential hatchling recruitment was 1300–2500 turtles/yr (Fig. 1). After foxes were removed, annual recruitment increased to 7000–8500 hatchlings. Almost 16000 hatchlings entered treatment populations after foxes were reduced in 1998 and 1999, whereas fewer than 4000 hatchlings entered the control population during the same period (excluding transplanted hatchlings; see Fig. 1).

Although overall size distributions of turtles captured in both Bankview (low-recruitment) and Hawkview (high-recruitment) lagoons did not differ before (January 1997) and five years after (January 2002) fox removal, the number of captures of turtles with PL = 110–150 mm (plastron length) spiked in Hawkview

lagoon in January 2002 (Fig. 2). This size range corresponds to a turtle age of 3–5 years (Fig. 3).

### Growth

From a total catch of 1339 juvenile and female *E. macquarii*, individual growth coefficients ( $k$ ) at all sites were similar prior to fox removal. After foxes were removed, individual growth rates were greater in fox removal (high-recruitment) populations compared to the control population (Table 1). Asymptotic length ( $a$ ) decreased in all populations, but all estimations were within similar confidence limits (Table 1).

The relationship between growth and both incubation temperature and population density depended on age

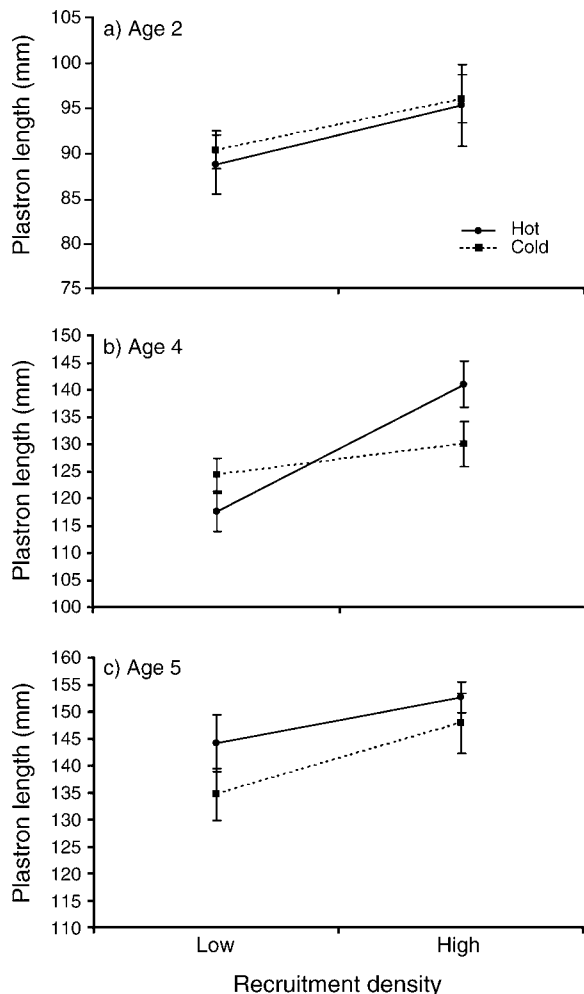


FIG. 3. Interaction between density and incubation temperature on growth (plastron length, mean  $\pm$  se) at ages 2, 4, and 5 years in *E. macquarii*. Plastron length was greater in high-recruitment sites than low-recruitment sites in most years. Incubation temperature affected growth in the high-recruitment site in year 4 (b), but turtles incubated in the hot treatment (solid line) were larger than turtles incubated in the cold treatment (dashed line) in both high- and low-recruitment treatments.

TABLE 1. Nonlinear regression of recapture data for the turtle *Emydura macquarii* from each control and treatment population (before and after fox removal) fitted to von Bertalanffy logistic equations.

Site and treatment	Pre-removal				Post-removal			
	<i>k</i>	<i>a</i>	RMS	<i>n</i>	<i>k</i>	<i>a</i>	RMS	<i>n</i>
Bankview (control)	0.12 (0.10–0.14)	219 (211–229)	8.1	101	0.14 (0.13–0.16)	214 (208–224)	6.1	312
Hawksview (high recruitment)	0.11 (0.10–0.12)	221 (210–232)	6.1	115	0.19 (0.18–0.21)	215 (206–224)	5.9	356
Snowdon's (high recruitment)	0.11 (0.09–0.13)	218 (209–227)	6.1	123	0.22 (0.20–0.24)	212 (206–229)	4.9	332

Notes: Estimates and 95% confidence intervals are given for the asymptotic plastron length constant (*a*) and the characteristic growth coefficient (*k*). RMS is root mean square. Growth constants were lower in the control site but increased after fox removal in the treatment sites.

(Table 2). A three-way ANCOVA revealed that there was an Age  $\times$  Incubation temperature  $\times$  Density interaction and that hatchling PL had no effect on post-hatching growth. We then removed age as a treatment and PL as a potential covariate, and conducted separate two-way ANOVAs for each age group to further explore the meaning of this result. Density at all ages had a significant effect on growth, but incubation temperature became increasingly important as turtles aged (Table 2). At all ages, individual growth was generally greater in the high-recruitment population compared to the low-recruitment population, but the relationship depended on incubation temperature at ages 4 and 5 (Fig. 3). There was no significant difference in growth at age 4 between density treatments for turtles incubated under colder conditions during embryonic development. However, turtles incubated under the hotter regime were significantly larger in the high-recruitment population compared to their sibs in the low-recruitment population ( $t_4 = 6.5$ ,  $P < 0.001$ ). Within the low-recruitment population at age 4, there was no difference in growth of turtles incubated at either temperature (Fig. 3). However, turtles from the hotter incubation temperature were larger than turtles from the colder incubation temperature within the high-recruitment treatment ( $t_3 = 3.6$ ,  $P < 0.01$ ). At age 5, turtles incubated at both hotter ( $t_8 = 3.5$ ,  $P = 0.002$ ) and colder ( $t_6 = 6.6$ ,  $P < 0.001$ ) incubation temperatures were larger in the high-recruitment than in the low-recruitment population. Although there was a significant difference between growth of hot- and cold-incubated turtles in the low-recruitment population at age 5 ( $t_8 = 5.6$ ,  $P < 0.001$ ), there was no such difference in the high-recruitment population (Fig. 3).

Regardless of environmental effects on growth, there was a strong genetic (family) correlation underlying body size of young turtles between density treatments. However, the shapes of those genetic relationships were related to age (Fig. 4). Slopes were significantly different at age 5 ( $b = 1.71 \pm 0.48$ ; all values mean  $\pm$  SE;  $r_G = 0.78$ ,  $F_{1,8} = 12.1$ ) compared to age 4 ( $b = 0.44 \pm 0.15$ ;  $r_G = 0.77$ ,  $F_{1,6} = 8.9$ ) and age 2 ( $b = 0.58 \pm 0.16$ ;  $r_G = 0.77$ ,  $F_{1,9} = 12.8$ ), indicating ontogenetic changes in genetic covariance for juvenile body size.

#### Survival

In the high-recruitment site, annual survival of released hatchlings was related to size at hatching ( $\phi(\text{PL})_t$  QAIC<sub>c</sub> weight = 1.0,  $\Delta\text{QAIC}_c = 28.0$ ) and was generally lower than estimates of survival of hatchlings released into the low-recruitment population, although overall recapture probabilities over time were low ( $p_t = 0.10\text{--}0.23$ ) (Fig. 5). In the low-recruitment site, annual survival was constant at 0.57 (with 0.12–0.78 95% CI) and unrelated to hatching size ( $\phi p_t$  QAIC<sub>c</sub> weight = 0.95,  $\Delta\text{QAIC}_c = 5.9$ ). Again, recapture rates over the duration of the study were low ( $p = 0.09\text{--}0.28$ ). Thus, although size at hatching was unrelated to post-hatching growth, larger neonates in the high-recruitment site accrued a survival advantage over smaller individuals and benefited from the opportunity for rapid growth produced by that presumably competitive post-hatching environment.

#### DISCUSSION

Our data clearly support the concept that juvenile growth in *Emydura macquarii* represents adaptive phenotypic plasticity and is optimized. In this case, we

TABLE 2. Results of two-way ANOVA of the effects of incubation temperature (Inc. temp.) and population density (Density) on growth rate (plastron length) at ages 2, 4, and 5 years in *Emydura macquarii*.

Variable	Age 2			Age 4			Age 5		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Inc. temp.	1	0.0	0.9	1	0.9	0.4	1	28	<0.001
Density	1	18	<0.001	1	36	<0.001	1	53	<0.001
Inc. temp. $\times$ Density	1	1.1	0.3	1	17	0.006	1	7.1	0.013
Residual	16			6			24		
Total	19			9			27		



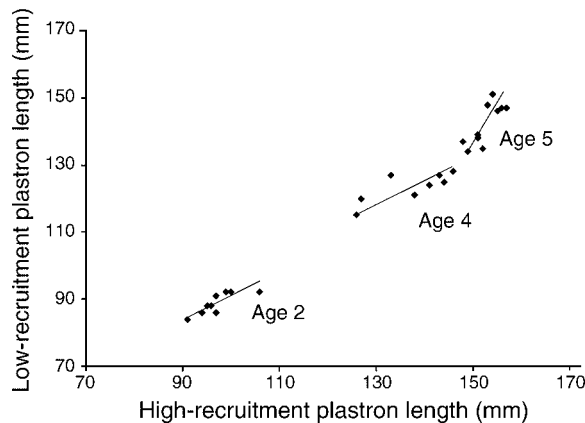


FIG. 4. Genetic (family) correlation of body size across both low- and high-density populations. A high positive association between populations occurred in all years, but the slope for five-year-old turtles was significantly different from two-year and four-year groups.

rejected the resource-limiting hypothesis because growth rates were greater in the high-recruitment population compared to the low-recruitment population. Submaximal growth in organisms has often been described as growth optimization, with the prediction that the optimal use of resources is a delicate trade-off among growth, maintenance, and reproduction (Arendt and Reznick 2005). Although plastron length at hatching was not a good predictor of growth rate; it predicted which turtles survived in the high-recruitment population. Positive selection for rapid growth occurred in the high-recruitment population because the growth rate response was related to size-dependent differences in mortality from competitive inter- and intraspecific interactions or predation. In our study, we suspect that the reduction in foxes at the experimental sites may have promoted higher mortality of juvenile turtles by predators otherwise inhibited by the presence of foxes, e.g., corvids and rodents (*Hydromys chrysogaster*). Indeed, mortality of juvenile turtles was generally higher at Hawksview than at Bankview and was positively size dependent in the former population. In this way, selection strongly favored an elevated growth rate of juvenile turtles observed at Hawksview, supporting the mortality hypothesis for life-history evolution in this long-lived turtle species.

Most life-history models have assumed that selection should favor a maximization of juvenile growth rate, because individuals with rapid growth have the potential to reach the largest possible size in the shortest possible time (Gotthard 2001). Under this hypothesis, growth rate is directly determined by environmental quality, which depends on factors such as food availability and ambient temperature (Gibbons 1967, Avery et al. 1993, Gottard 2001). However, theory predicts that rapid growth is costly. Growth is part of a suite of genetically coupled fitness traits that have coevolved. Due to

negative genetic correlations, higher growth rates are costly because energy is channeled into growth and away from other traits. There is strong evidence that individuals can grow at a slower rate than they are physiologically capable of achieving (Case 1978, Arendt 1997, Nylin and Gotthard 1998, Bronikowski 2000), and this study highlights the context dependency of size-related survival. Where there is a premium on size, larger size should be favored by selection, but when survival is high or resources are abundant, larger neonatal body size is unlikely to confer substantial fitness benefits (Janzen 1993, Congdon et al. 1999). A submaximal, or reduced, pattern of growth is observed in the low-recruitment population because high growth rates actually may be associated with a fitness cost; the optimal growth rate of an individual in this environment is not necessarily maximal (Gotthard 2001). Life-history theory predicts that the components of the energy budget compete with one another for available resources and the costs of rapid growth may be developmental, behavioral, or physiological (Gadgil and Bossert 1970). In other species, rapid growth is achieved through higher rates of energy acquisition (Nicieza et al. 1994, Jonassen et al. 2000). However, longevity is one trait that characterizes the life-history pattern of turtles, and greater energy acquisition essentially requires changes in feeding behavior or a complete habitat shift, which increases the risks in obtaining food (Skelly 1994). Similarly, diverting energy from other somatic processes to growth has long-term impacts on aging and longevity (Jonsson et al. 1992), energy storage (Forsman and Lindell 1991), and resistance to pathogens (Smoker 1986). In fact, negative selection for rapid growth may occur in these environments; both theoretical and empirical studies of adaptive growth imply that the

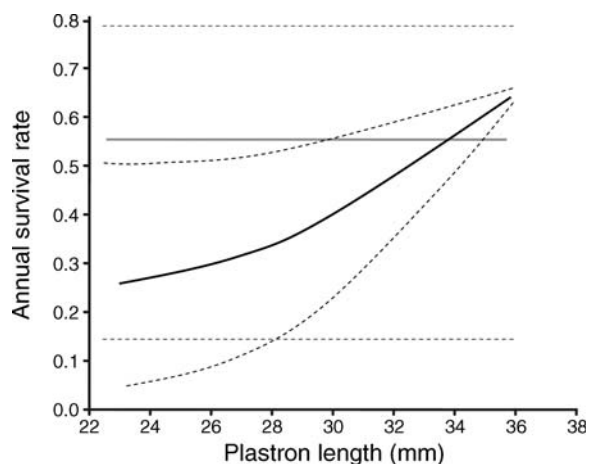


FIG. 5. Annual survival rate (mean with 95% CI shown as dashed lines) in relation to body size of hatchlings released into the high- and low-recruitment populations. Survival was positively related to hatching size in the high-recruitment population (black line) but was constant in the low-recruitment population (gray line).

benefits of slower growth in populations of low recruitment or density may be obtained through increased longevity (Spencer and Thompson 2005) and lower rates of reproductive and cellular senescence (Congdon et al. 2001).

Although growth is submaximal in low-recruitment population, is it optimized? Most models of optimal age and size at maturity have not incorporated the possibility that individuals adaptively adjust their growth by balancing it against juvenile mortality (reviewed in Roff 1992, Stearns 1992). Gilliam and Fraser (1987) suggested that the optimal growth strategy of an individual is to choose habitats that minimize the ratio of mortality rate ( $\mu$ ) and growth rate ( $g$ ): the “minimize  $\mu/g$ ” rule. Assuming mean annual mortality rates of 0.59 and 0.43 in the high- and low-recruitment populations, respectively (Fig. 5), and  $k$  values from Table 1, the respective  $\mu/g$  ratios were 2.95 and 3.07. These ratios are very similar, suggesting that growth may be optimal in both environments, at least at the population level.

Growth in reptiles is influenced by several factors, including the maternal effects of egg size and egg quality (Congdon and Gibbons 1985, Packard and Packard 1988, Bernardo 1996, Steyermark and Spotila 2001), and environmental variables, such as incubation temperature and substrate water potential (Ewert 1985, Packard and Packard 1988). Thermal and hydric conditions during incubation can influence locomotion (Van Damme et al. 1992), defense (Burger 1998), and survival of hatchling ectotherms (de March 1995), and thereby indirectly impact juvenile growth as well. These consequences of the incubation environment for offspring quality can last for years (Joanen et al. 1987, Roosenburg and Kelley 1996). Indeed, our field experiments revealed a remarkably delayed long-term impact of the thermal conditions experienced during embryonic development on growth of turtles prior to maturity. Moreover, this thermal effect was manifested in turtles approaching maturity, rather than in turtles closer to hatching, and was dependent on the population density in the post-hatching rearing environment. The delayed effect of incubation temperature on post-hatching growth may be linked to temporal changes in gene expression related to both developmental and environmental conditions (e.g., Cheverud et al. 1996, Atchley and Zhu 1997). At all ages, we detected a strong positive genetic correlation between density treatments, but the slope of this relationship changed with age (Fig. 5). Of particular note, larger turtles in the high-recruitment treatment exhibited slowed growth rates at age 5, an indicator of the approaching onset of maturity. Why this pattern arose is not clear, but we can rule out one possible explanation. Most turtles have temperature-dependent sex determination, in which warm incubation temperatures yield females and cool incubation temperatures produce males (Ciofi and Swingland 1997). *Emydura macquarii* does not have this sex-determining mechanism

(Thompson 1988), so incubation temperature cannot be confounded with sex in this study. Hence, our results are not caused by sex-specific growth. We expect that both males and females are distributed across all treatments, and we will explicitly assess sex-specific differences in growth once individuals reach maturity over the next five years.

Although our experimental design cannot rule out possible non-genetic maternal effects on post-hatching growth, their influence is likely to be minimal in this study. In some turtles, the maternal effect of egg mass influences offspring size and subsequent post-hatching growth (e.g., Roosenburg and Kelley 1996, Janzen and Morjan 2002). Similarly, egg size is positively related to hatchling body size in *E. macquarii* (Judge 2001), but such non-genetic maternal effects do not appear to affect post-hatching growth: we found that growth in all years was never dependent on body size at hatching. Our findings accord with those noted for garter snakes, where maternal effects on body size at birth are important (Bronikowski and Arnold 1999), but are negligible on neonatal growth (Bronikowski 2000). In addition, our transplant experiment was designed to minimize the influence of non-genetic maternal effects on among-clutch variation in juvenile growth, because hatchlings were obtained from females that inhabited a common environment.

In conclusion, our experimental populations experienced a dramatic change in demographic structure as increased numbers of juveniles were recruited. At the same time, juveniles in these high-recruitment populations were not resource limited, growing more rapidly than young turtles in the control population, while experiencing higher mortality. This apparent phenotypic plasticity in juvenile growth is complemented by our observation of a strong, positive genetic correlation between individual body size in the experimental and control populations ( $r_G \sim +0.77$  at each age). Genetic correlations across environments quantify the degree to which expression of a trait in one environment shares a heritable genetic basis with the expression of the same trait in another environment (Via and Lande 1985). Thus, these Australian pleurodiran turtle populations seem to have the impressive capacity to acclimate plastically to major demographic perturbations as well as the longer-term potential to evolve adaptively.

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